

STYRACACEAE HARDY IN TEMPERATE NORTH AMERICA¹

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STYRACACEAE Dumortier, Anal. Fam. 28, 29. 1829, "Styracineae," nom. cons.

(STYRAX FAMILY)

Evergreen or deciduous trees or shrubs, usually with stellate (or lepidote) pubescence. Leaves simple, alternate, exstipulate, with entire, serrate, dentate, or occasionally lobulate margins, the venation pinnate. Flowers perfect, actinomorphic; inflorescences often reduced, the flowers usually arranged in simple or sometimes branched, terminal and/or axillary racemes, corymbs, or panicles, occasionally solitary or in few-flowered fascicles. Calyx often articulated at the base, synsepalous, tubular, subentire or 4- or 5-toothed or -lobed; calyx tube entirely free to completely adnate to the ovary. Corolla sympetalous, 4- or 5-lobed (rarely more), often united into a tube only at the base; insertion of the corolla hypogynous (ovary superior) to epigynous (ovary inferior), the lobes valvate or imbricate in bud. Stamens usually twice the number of the corolla lobes, sometimes more, epipetalous, inserted in 1 whorl on the base of the corolla (or rarely at the base of the ovary), the filaments usually connate into a tube below, free above; anthers 4-locular. Gynoecium syncarpous,

¹This treatment of the Styracaceae is the second contribution in a series of treatments of cultivated ligneous plants, the preparation of which is a project of the Arnold Arboretum of Harvard University and the purpose of which is to provide a modern, accurate account of the woody plants encountered in cultivation in the cooler temperate regions of North America. It is hoped that these treatments will eventually form the basis of a new manual of cultivated woody plants. The first paper in this series was published in the *Journal of the Arnold Arboretum* 56: 1-19. 1975. Reference should be made to the introductory paragraphs of that paper for matters concerning area covered, taxa included, and the general philosophy of these treatments.

For their numerous contributions of time, advice, knowledge, and encouragement in this project, I am especially indebted to Drs. R. A. Howard, B. G. Schubert, P. F. Stevens, C. E. Wood, Jr., and R. E. Weaver, Jr. I should also like to thank Dr. L. M. Perry for her invaluable help with numerous problems, Mrs. I. H. Burch for her interest in and preliminary studies of *Halesia* and *Pterostyrax* in the living collections of the Arnold Arboretum, and Miss K. Clagett for her editorial assistance. The illustrations are the careful work of Robin S. Lefberg and were prepared, when possible, from living or alcohol-preserved specimens collected in the Arnold Arboretum. These collections were made by R. E. Weaver, Jr., M. Gilmore, I. H. Burch, and myself. Additional alcohol-preserved specimens collected by C. E. Wood, Jr., and R. B. Channell from wild populations and from plants in the living collections of the Henry Foundation for Botanical Research, Gladwyne, Pennsylvania, have been utilized. These materials were collected for the Generic Flora of the Southeastern United States project and were kindly made available for use by Professor Wood.

Special thanks and gratitude are also extended to an anonymous donor, whose generous gift for this project has made and continues to make this work possible. In addition, our deepest thanks are extended to the Director and trustees of the Stanley Smith Horticultural Trust for a grant that has made possible the preparation of illustrations to accompany these treatments. S. A. S.

the ovary superior and completely free to inferior and completely adnate to the calyx tube, 3–5-locular, often 1-locular above, each locule with 1 to many ovules on axile placentae; style 1, slender, terminated by a usually 3–5-lobed stigma. Fruits dry, often woody, indehiscent or dehiscent; seeds 1 to many, the usually straight embryo with broad cotyledons embedded in fleshy endosperm. TYPE GENUS: *Styrax* L.

Thirteen genera and about 150 species distributed primarily in eastern Asia to western Malesia, tropical South America, and North America, primarily in the southeastern United States. One species (*Styrax officinale* L.) occurs in the Mediterranean region, while about three additional species are native to Africa.

The genus *Sinojackia* H. H. Hu, included by Rehder (1942) in his *Manual*, has been excluded from the present treatment, since evidence of its hardiness and cultivation in our area has not been located. Apparently, only *S. rehderiana* Hu is grown in North America at the present time; we have records of its inclusion in the collections of the Strybing Arboretum in San Francisco.

Closely related to *Rehderodendron* and *Pterostyrax*, *Sinojackia* is distinguished from both of these genera by its flowers on slender pedicels in 3–5-flowered racemes terminating leafy, lateral branches, by its stamens with the connectives produced beyond the anthers, and by its ovoid, woody, unribbed fruits, 1.5–2.5 cm. long.

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KEY TO THE GENERA OF STYRACACEAE IN CULTIVATION

1. Ovary \pm inferior, adnate to the calyx tube; insertion of the corolla epigynous; fruits sometimes surmounted by the persistent calyx lobes; pedicels articulated at the base of the calyces. 2.

2. Pith chambered; flowers solitary, in few-flowered fascicles, or rarely in irregular racemes above leaf scars on second-year branchlets; corolla with 4 or rarely 5 lobes; fruits conspicuously 2- or 4-winged. 1. *Halesia*.
2. Pith continuous; flowers in racemose or paniculate inflorescences above leaf scars on second-year branchlets or in paniculate or corymbiform inflorescences terminating short, lateral branchlets from second-year wood; corolla with 5 lobes; fruits obscurely ribbed, 5-winged, or large, woody, and variously ribbed, or smooth. 3.
3. Stamens subequal; flowers several to numerous, in paniculate or corymbiform inflorescences terminating short, lateral branchlets; fruits small, 8–17 mm. long, obscurely ribbed or 5-winged. 2. *Pterostyrax*.
3. Stamens of 2 unequal lengths; flowers few, in racemose or paniculate inflorescences above leaf scars; fruits large, (4–)6–8.5 cm. long, smooth or variously ribbed, not winged. 3. *Rehderodendron*.
1. Ovary \pm superior, usually adnate basally to the calyx tube, rarely entirely free; insertion of the corolla hypogynous to perigynous; fruits subtended by the persistent calyces; pedicels not articulated at the base of the calyces. 4. *Styrax*.

1. *Halesia* Ellis ex Linnaeus, Syst. Nat. ed. 10. 2: 1044, 1369. 1759, nom. cons.²

Deciduous trees or shrubs, the branchlets with chambered pith; winter buds ellipsoidal to ovoid, pubescent; bark brownish, gray, or blackish, becoming deeply cleft on older trees. Leaves petiolate, the blades chartaceous, ovate-oblong, elliptic, or obovate, with acute to acuminate apices, serrate or serrulate margins (the veins ending in apiculate teeth), and rounded, cuneate, or attenuate bases; surfaces of the blades usually densely stellate-pubescent when young, sometimes becoming glabrous. Flowers usually drooping on slender pedicels, solitary, in fascicles of 2–8 flowers, or in short irregular racemes; fascicles or racemes occurring above leaf scars on second-year branchlets. Calyx tube 4- or rarely 5-toothed or subentire, the tube \pm completely adnate to the ovary; pedicel articulated at the base of the calyx. Corolla expanding prior to anthesis, initially greenish, becoming white to pale pink, campanulate, 4- or rarely 5-lobed or deeply cleft nearly to the base. Stamens 8–16, included or exerted, the filaments coherent basally for part of their length and adnate to the corolla. Gynoecium 2–4-carpellate; ovary \pm completely inferior, 2–4-locular, each locule with 4 ovules on axile placentae; style simple, slender, terminating in a minute, sometimes 4-lobed stigma. Fruits dry, glabrous, and indehiscent, clavate, oblong, or \pm ellipsoidal, prominently 2- or 4-winged, terminated by the persistent style base. Seeds 1–4 per fruit, solitary in each locule through abortion, surrounded by a stony covering. (*Mohria* Britton, non Swartz; *Mohrodendron* Britton; *Carlo-*

²This treatment is adapted from that of E. W. Chester, 1966.

mohria Greene.) TYPE SPECIES: *H. carolina* L. (Name honoring Stephen Hales, 1677–1761, English botanist and author of *Vegetable Staticks*, an early treatise on plant physiology.) — SILVERBELL-TREE, SNOWDROP-TREE.

Three species of the southeastern United States, one comprised of two varieties, and *Halesia macgregorii* Chun of southeastern China. With the exception of *H. macgregorii*, all the species are known in cultivation.

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KEY TO THE SPECIES OF HALESIA IN CULTIVATION

1. Corolla shallowly 4-(5-)lobed, the lobes less than $\frac{1}{2}$ the length of the campanulate corolla (or rarely cleft nearly to the base); stamens 8–16; fruits 4-winged; leaves generally 2 times or more longer than broad. 2.
2. Stamens exserted from the corolla at anthesis; corolla 8–15 mm. long; fruits clavate, narrowly tapered to the base. 1. *H. parviflora*.
2. Stamens included within the corolla at anthesis; corolla 13–22 mm. long; fruits ellipsoidal with broad, rounded bases, rarely \pm clavate. 2. *H. carolina*.
1. Corolla deeply cleft almost to the base into 4 (or 5) petal-like lobes; stamens usually 8, rarely to 16; fruits broadly 2-winged; leaves generally less than 2 times as long as broad. 3. *H. diptera*.

1. *H. parviflora* Michaux, Fl. Bor.-Am. 2: 40. 1803. FIGURE 1, d-f.

Shrubs or small trees to ca. 10 m., with dark, blackish-brown bark fissured into narrow ridges; branchlets reddish-brown, obscurely stellate-pubescent, becoming glabrous. Petioles 0.5–1.9 cm. long; leaf blades oblong-ovate to elliptic, 6–17 cm. long, 2.5–8 cm. wide, with acute to acuminate apices, serrulate margins, and cuneate to rounded bases; upper and lower surfaces whitened by stellate hairs when young, at maturity dull green, pubescent or glabrous above, finely stellate-pubescent below, particularly along the primary veins. Flowers long-pedicellate, appearing in spring with the leaves, usually 3 or 4 together in fascicles or occasionally in irregular short racemes; pedicels and calyces 6–15 mm. long, the calyx tube subentire or 4-toothed; corolla white, campanulate, shallowly 4-lobed, 8–15 mm. long; stamens 8–16, equal, exserted from the corolla at anthesis; style elongate, exserted, usually exceeding the stamens; ovary inferior, 2–4-loculate. Fruits clavate, terminated by the persistent style base, gradually narrowed to the base, 2–4 cm. long, with 4 narrow, \pm equal wings. $2n = 24$. (*Halesia tetraptera* L. var. *parviflora* (Michx.) Schelle; *H. tetraptera* Ellis, *sensu* Godfrey; *Mohrodendron parviflorum* (Michx.) Britton.) — LITTLE SILVERBELL, FLORIDA SILVERBELL.

Native to the Coastal Plain of the southeastern United States in South Carolina, Georgia, northern Florida, Alabama, and Mississippi.

2. *H. carolina* Linnaeus, Syst. Nat. ed. 10. 1044. 1759. FIGURE 1, a-c.

Small trees, often with several trunks from near the base, to 10 m., or occasionally large trees with a single trunk to 30 m.; bark bluish-gray with longitudinal whitish or buff-colored streaks, becoming rough and ridged in old specimens; branchlets with blackish bark exfoliating in thin, longitudinal strips. Petioles stout, 0.7–2.4 cm. long; leaf blades ovate to ovate-oblong, 9.5–22.5 cm. long, 4.5–9.8 cm. wide, with acute, short- or long-acuminate apices, finely serrulate margins, and cuneate to rounded bases; blades finely and often densely stellate-pubescent when young, at maturity bright green and puberulous above, pale green, glabrous or finely stellate-pubescent, particularly along the veins, below. Flowers borne on slender, drooping pedicels, appearing in spring with expanding leaves, in 3–8-flowered fascicles, in short, congested racemes, or rarely solitary; pedicels and calyces 1–2.3 cm. long, the calyx tube obconic, with 4 deltoid or obsolete lobes; corolla white, white flushed with pink, or pink, campanulate, 1.3–2.2 cm. long, with 4 shallow lobes (or rarely cleft to below the middle); stamens 8–16, equal, included within the corolla; ovary inferior, 4-locular, the slender style included or exserted. Fruits green, becoming reddish-brown, usually ellipsoidal, terminated by the persistent style base, rounded or tapered slightly at base, 2–6 cm. long, with 4 broad to narrow wings. $2n = 24$. (*Halesia tetraptera* Ellis; *H. tetraptera* L.; *Mohrodendron carolinum* (L.) Britton; including *H. tetraptera* f. *meehanii* Meehan ex Sarg., *H. carolina* f. *dialypetala* (Rehder)

Schneider, *H. carolina* var. *mollis* (Lange) Perkins, *H. monticola* (Rehder) Sarg., *H. monticola* var. *vestita* Sarg., and *H. monticola* var. *vestita* f. *rosea* Sarg.) — SILVERBELL-TREE, SNOWDROP-TREE.

Native to the southeastern United States from West Virginia and Virginia south to South Carolina and northern Alabama, and westward through Kentucky, Tennessee, and southern Ohio to Illinois, Arkansas, and Oklahoma.

Variable in habit (small, shrublike trees, often with several trunks from the base, to large, single-trunked trees), flower size and color (white, white flushed with pink, or pinkish throughout), and leaf size and pubescence, *Halesia carolina* has been treated as comprised of several varieties or has been divided into two closely related species, each with a number of subordinate taxa. The majority of these taxa, moreover, have been recognized at one time or another by botanists, horticulturists, and nurserymen, resulting in a confused and awkward taxonomy. Recent studies by Chester (1966), however, show that the characters used to define these taxa (regardless of the rank assigned to them) are either clinal over portions of the geographic range of the complex or exhibit random variation without correlations worthy of taxonomic recognition. As a result, *H. carolina* is treated here as a single, variable species without a constellation of varieties or forms.

Two names placed in synonymy have previously been considered as cultivars. Forma *meehanii* Meehan ex Sarg. (Gard. Forest 5: 534. 1892) (*H. carolina* L. var. *meehanii* (Meehan ex Sarg.) Perkins, Pflanzenr. IV. 241(30): 97. 1907) (= cv. *Meehanii*), a small bushy tree, was described from a plant that appeared as a seedling. Chester considers this plant to be a teratological form of *H. carolina* with short-pedicellate flowers, small, cup-shaped corollas, and thickish, rugose leaves. In addition, plants of *H. monticola* var. *vestita* Sarg. (Jour. Arnold Arb. 2: 171. 1921) with pink flowers have been designated as f. *rosea* Sarg. (*loc. cit.*) (= cv. *Rosea*) and have also been considered as a cultivar of *H. carolina*. It should be noted, however, that evidence presented by Chester indicates that the pink coloration of the corollas is subject to environmental modification (the pink color is developed in the absence of direct sunlight) and is also partially a function of the age of the flower. It is questionable, therefore, whether corolla color would remain true unless clonal progeny were grown under certain environmental conditions.

3. *H. diptera* Ellis, Phil. Trans. Roy. Soc. London 51: 931, 932. *t.* 22, *fig. b.* 1761. FIGURE 1, g, h.

Shrubs or small trees to 10 m.; bark reddish-brown, flaking into small, thin scales and irregularly longitudinally fissured; branchlets grayish or brownish, lustrous, with scattered stellate hairs, becoming glabrous and purplish-black. Petioles 1–3.3 cm. long; leaf blades ovate to obovate, 8.5–18 cm. long, 4.5–10.8 cm. wide, with acuminate apices, denticulate-serrate margins, and rounded to cuneate bases; blades light green, pubes-

cent along the veins above, pubescent over the entire surface below, particularly along the conspicuous, reticulated veins, often becoming \pm glabrous with age. Flowers occurring with the leaves in spring, long-pedicellate, 2–6 together in fascicles or in short racemes; pedicels and calyces 1–1.8 cm. long, the calyx tube obconic with deltoid lobes; corolla white, 0.9–1.7 cm. long, deeply divided nearly to the base into 4 (rarely 5) ovate or obovate lobes; stamens usually 8 (or sometimes to 16), equal, included; ovary 2- or rarely 4-locular, the style elongate, slender, included. Fruits reddish-brown, compressed, oblong, terminated by the persistent style base, 2.5–5 cm. long, with 2 conspicuous broad wings. $2n = 24$. (*Mohrodendron dipterum* (Ellis) Britton.) — SNOWDROP-TREE.

Native to the Atlantic and Gulf coastal plains of the southeastern United States from South Carolina to eastern Texas.

Plants with larger flowers (the corolla 2–3 cm. long and the pedicel and calyx 1.6–2.8 cm. long) have been recognized as var. *magniflora* R. K. Godfrey (*Rhodora* 60: 88. 1958). This variety occurs naturally in rich deciduous woodlands of southern Georgia, in the panhandle of northern Florida, and in southern Alabama.

2. *Pterostyrax* Siebold & Zuccarini, Fl. Jap. 1: 94. 1839.

Deciduous trees or shrubs, the branchlets with continuous pith; winter buds enclosed by 2 overlapping, stellate-pubescent scales. Leaves petiolate, the blades chartaceous, elliptic, ovate, or oblanceolate, with entire to serrate or denticulate margins (the veins ending in apiculate teeth), attenuate to rounded bases, and acute, short-acuminate, or truncate and 3-lobed apices; upper surfaces variously pubescent, sometimes glabrescent; lower surfaces stellate-pubescent, occasionally with simple hairs along the veins. Flowers several to numerous, \pm secund in densely stellate-pubescent paniculate or corymbiform inflorescences terminating short lateral branchlets from second-year wood; pedicels articulated at the base of the calyx. Calyx adnate to the ovary, with 5 teeth or lobes. Corolla white, deeply cleft almost to the base into 5 lobes. Stamens 10, exserted, the filaments connate basally for a portion of their length. Gynoecium 3-, rarely 4- or 5-carpellate; ovary inferior, 3- (4- or 5-)locular, each locule with 4 ovules; style simple, exserted, with a small, persistent annular disc at its base. Fruits indehiscent, subglobose to clavate, winged or ribbed, variously pubescent. Seeds 1 or 2, tightly enclosed in the fruit. (Including *Decavenia Koidzumi*.) TYPE SPECIES: *P. corymbosa* Sieb. & Zucc. (Name from Greek *pteron*, wing, and *Styrax*, the closely allied genus, in reference to the winged fruits of the type species.)

Four or five species of eastern Asia in Japan, China, and Burma. In addition to the two species treated below, *Pterostyrax psilophyllus* Diels and *P. leveillii* Chun have been described from China, while *P. burmanicus* Smith & Farrer is native to Burma.

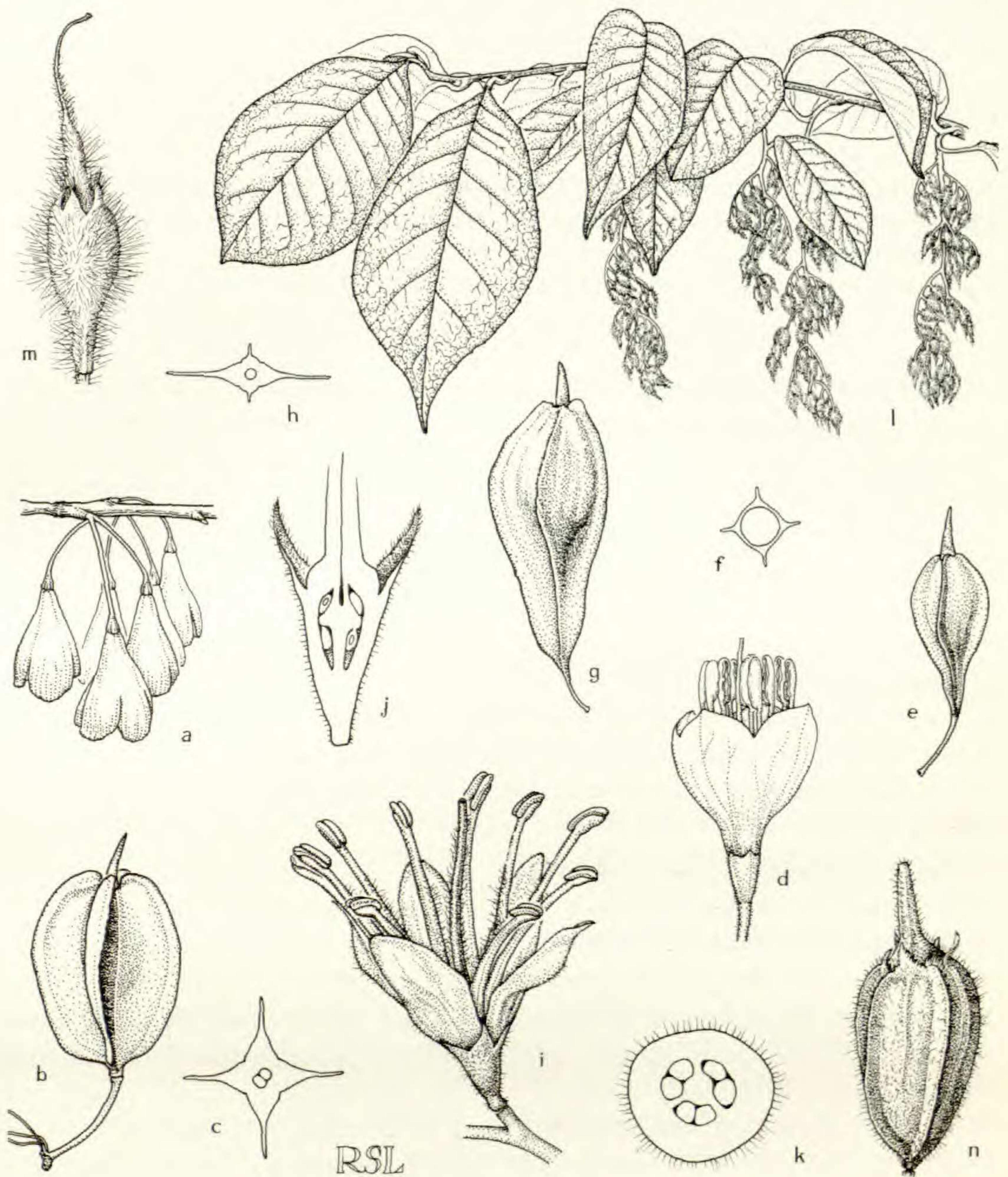


FIGURE 1. *Halesia* and *Pterostyrax*. a-h, *Halesia*. a-c, *H. carolina*: a, habit, showing fascicles of flowers, $\times \frac{3}{4}$; b, four-winged fruit, $\times \frac{3}{4}$; c, cross-section of fruit, showing the four \pm equal wings, $\times \frac{3}{4}$. d-f, *H. parviflora*: d, flower at anthesis, showing stamens exerted from the corolla, $\times 1\frac{1}{2}$; e, pyriform, four-winged fruit, $\times \frac{3}{4}$; f, cross-section of fruit, showing the four \pm equal wings, $\times \frac{3}{4}$. g, h, *H. diptera*: g, fruit, showing the two large wings, $\times \frac{3}{4}$; h, fruit in cross-section, showing the two large and 2 small wings, $\times \frac{3}{4}$. i-n, *Pterostyrax*. i-m, *P. hispida*: i, flower at anthesis, note articulation at base of calyx, $\times 3$; j, longitudinal section of flower (corolla and androecium removed), $\times 6$; k, cross-section of ovary, showing 3-locular condition, $\times 12$; l, habit, showing pendent infructescences, $\times \frac{1}{4}$; m, individual fruit, showing long, bristlelike hairs, $\times 3$. n, fruit of *P. corymbosa*, $\times 3$.

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KEY TO PTEROSTYRAX HISPIDA AND PTEROSTYRAX CORYMBOSA

1. Flowers in pendent, secund, paniculate inflorescences (8-)10-20 cm. long; calyx lobes deltoid; lower surfaces of the leaf blades stellate-pubescent, usually with long, simple hairs along the veins; young branchlets glabrous; fruits finely ribbed, stellate-pubescent and beset with longer, stiff, yellowish-brown simple hairs. 1. *P. hispida*.
1. Flowers in drooping, ± secund, corymbiform inflorescences 6-8 cm. long; calyx lobes subulate; lower surfaces of the leaf blades stellate-pubescent, without simple hairs along the veins; young branchlets loosely stellate-pubescent; fruits 5-winged, finely stellate-pubescent, lacking long, simple hairs. 2. *P. corymbosa*.

1. *P. hispida* Siebold & Zuccarini, Abh. Math-Phys. Cl. Akad. Wiss. München 4(3): 132. 1846; Fl. Jap. Fam. Nat. 2: 8. 1846.

FIGURE 1, i-m.

Trees or shrubs, often with several trunks from the base, to ca. 14 m., with brownish or grayish bark fissured in a checkered pattern; young branchlets reddish-brown, glabrous, the periderm on older growth exfoliating in thin strips. Leaf blades 7-14 cm. long, 2.5-6.5 cm. wide, oblong, obovate, or lanceolate, with attenuate bases, finely denticulate margins, and acute to attenuate apices; upper surfaces bright green with scattered simple hairs, particularly along the veins, becoming glabrous; lower surfaces pale, grayish-green, sparsely to densely stellate-pubescent over the entire surface and with simple hairs along the veins. Flowers secund in pendent paniculate inflorescences (8-)10-20 cm. long terminating short, lateral branchlets, often with reduced paniculate inflorescences in the axils of the subtending leaves; pedicels and calyces 4-5 mm. long, densely stellate-pubescent, the calyx lobes ± deltoid; corolla lobes 6-7 mm. long, linear-oblong, densely stellate-pubescent; stamens long-exserted, the filaments free nearly to the base; style exserted, exceeding the stamens. Infructescences pendent, the fruits (8-)10-15 mm. long, clavate, terminated by the persistent calyx lobes and style base; surface of the fruits finely ribbed, the ribs often obscured by fine stellate hairs and numerous long, stiff, yellowish-brown simple hairs. (*P. micrantha* Sieb. & Zucc.; *Decavenia hispida* (Sieb. & Zucc.) Koidzumi; *D. micrantha* (Sieb. & Zucc.) Koidzumi.) — EPAULETTE TREE.

Native to mountainous regions of Japan; also known from Hupeh and Szechwan provinces, China. With the exception of one collection, all herbarium sheets of cultivated *Pterostyrax* from North America examined during this investigation belong to this species. A handsome small tree or large shrub that blooms during June and July, *P. hispida* deserves to be more widely planted.

2. *P. corymbosa* Siebold & Zuccarini, Fl. Jap. 1: 96. t. 47. 1839.

FIGURE 1, n.

Shrubs or small trees with smooth, grayish bark; young branchlets with scattered stellate hairs, the periderm on older branchlets grayish-brown, exfoliating in thin strips. Leaf blades 4–9.5 cm. wide, 6–17 cm. long, ovate or obovate to broadly elliptic or oblanceolate, with rounded to attenuate bases, subentire, serrulate, or denticulate margins, and short-acuminate apices; upper surfaces pale green, finely stellate-pubescent, particularly along the veins, the lower surfaces with scattered stellate hairs. Flowers in short, drooping, \pm secund, corymbiform inflorescences 6–8 cm. long, terminating short, lateral branchlets, sometimes with small inflorescences in the axils of subtending leaves; pedicels and calyces 3–4 mm. long, densely stellate-pubescent, the calyx lobes subulate; corolla lobes 7–8 mm. long, linear-elliptic, densely stellate-pubescent; stamens exerted, the filaments connate, often forming a tube for most of their length; style exerted, about as long as or longer than the stamens. Infructescences drooping, the fruits 10–17 mm. long, narrowly 5-winged, terminated by the persistent basal portion of the style; surfaces of the fruits very finely stellate-pubescent. $2n = 24$. (*Halesia corymbosa* (Sieb. & Zucc.) Nicholson.)

Native to mountainous regions of Japan and Kiangsi and Hunan provinces, China; to our knowledge, documented as cultivated in North America by only one collection (*F. G. Meyer 13808*, May 12, 1973, AAH, NA) from a private garden in Maryland.

3. *Rehderodendron* H. H. Hu, Bull. Fan Mem. Inst. Biol. 3: 77.

pls. 1, 2. 1932.

Deciduous trees (and shrubs?), the branchlets with continuous pith; winter buds ovoid, with 2 or 3 finely stellate-pubescent outer scales. Leaves petiolate, the blades chartaceous to coriaceous, elliptic to oblong-ovate, with acute to acuminate apices, serrate or serrulate margins (the veins ending in apiculate teeth), and attenuate to \pm rounded bases; surfaces of the blades glabrous, glabrescent, or densely stellate-pubescent, particularly along the veins. Flowers borne on slender pedicels in leafless racemose or paniculate inflorescences above leaf scars on second-year branchlets. Calyx tube obconic, 5-toothed, the tube adnate to the ovary. Corolla white, occasionally flushed with pink, deeply 5-lobed nearly to the base. Stamens (8–)10, of 2 lengths, the filaments coherent at the

base and often adnate to the corolla or free. Gynoecium 3–5-carpellate; ovary \pm totally inferior, 3–5-locular, each locule with 4–6 ovules; styles simple, slender. Fruits large and woody, with thin, corklike exocarp and fibrous, spongy endocarp, indehiscent, glabrous or stellate-pubescent, oblong or ellipsoidal, unribbed and smooth or ribbed and sometimes deeply sculptured. Seeds 1–3, cylindrical. LECTOTYPE SPECIES: *R. macrocarpum* H. H. Hu; see H. H. Hu, Lingnan Sci. Jour. 12(suppl.): 112. 1933. (Name honoring Professor Alfred Rehder, Curator of the Arnold Arboretum, student of Chinese botany, and teacher of Chinese botanists, and from Greek *dendron*, tree.)

Perhaps ten species of eastern Asia in the temperate and subtropical regions of China and Indo-China. Although ten species have been described, it is doubtful that all would be maintained if the taxonomy of the genus were re-evaluated. Poorly represented in herbarium collections, the genus is infrequently encountered in cultivation; only the lectotype species is documented as grown in North America.

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1. *R. macrocarpum* H. H. Hu, Bull. Fan Mem. Inst. Biol. 3: 78. *pl.* 1. 1932. FIGURE 2, a–d.

Small trees to ca. 10 m. with grayish-black bark; young branchlets reddish-brown, glabrescent, the buds stellate-pubescent. Leaves membranaceous, 7–13 cm. long, 3.5–5.5 cm. wide, elliptic-ovate to oblong or lanceolate, with acute to acuminate apices, serrulate, red-tinged margins, and broadly cuneate to subrounded bases, the lamina sometimes decurrent along the short, glabrescent, scarlet petiole; upper surfaces green or reddish-green, glabrous, the lower surfaces paler green and stellate-pubescent along the reddish midvein and primary veins. Flowers borne on slender pedicels 3–10(–15) mm. long in short, few-flowered paniculate inflorescences; calyx tube ca. 4 mm. long, the lobes deltoid; corolla white (or apparently sometimes flushed with pink), the 5 lobes 10–15(–18) mm. long, ovate to elliptic, pubescent on both surfaces; stamens (8–)10, of 2 lengths, partly exserted; ovary inferior, the simple style about equalling the longer stamens. Fruits oblong-ovoidal, light reddish-brown, (4–)6–8.5 cm. long, 2.5–3 cm. in diameter, 8–10 ribbed, glabrous; seeds 1 or 2 through abortion, cylindrical, brown, ca. 5 cm. long.

Apparently endemic to a small area of Szechwan Province in western China, where the original collections of this species were made on Mount Omei between 1800 and 2000 meters.

4. *Styrax* Linnaeus, Sp. Pl. 1: 444. 1753; Gen. Pl. ed. 5. 203. 1754.

Evergreen or deciduous trees or shrubs, usually with several superposed winter buds with 1 outer scale; young branchlets commonly stellate-pubescent. Leaves subsessile to distinctly short-petiolate, the blades ovate, elliptic, oblong, lanceolate, or occasionally suborbicular, with subentire, serrate, dentate, or lobulate margins; surfaces of the blades glabrous or variously stellate-pubescent. Flowers arranged in axillary and/or terminal paniculate, racemose, or corymbose inflorescences, usually on short lateral branchlets and often with solitary or 2 to several flowers in the axils of subtending leaves. Calyx persistent, cuplike, 5- or rarely 6- or 7-

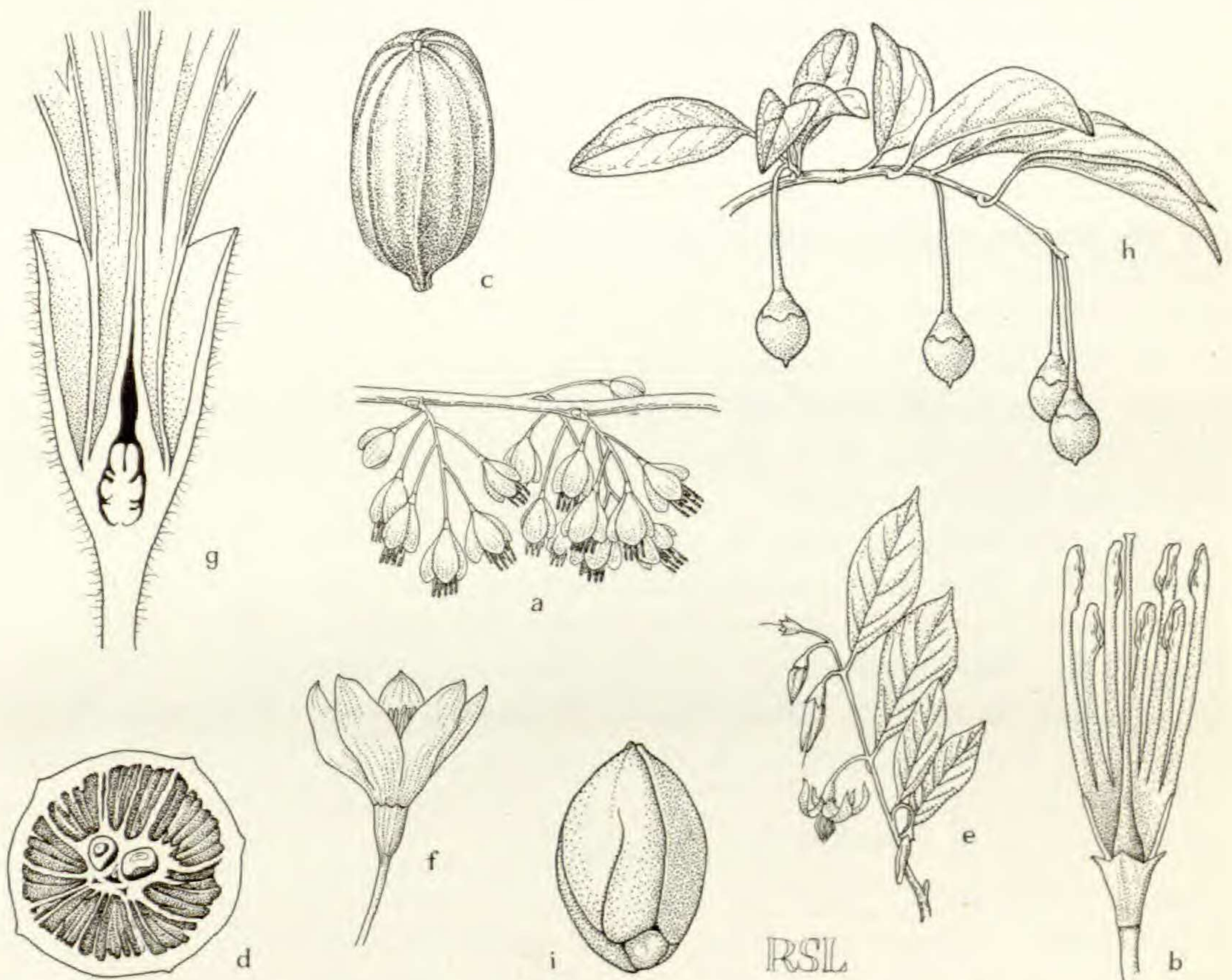


FIGURE 2. *Rehderodendron* and *Styrax*. a-d, *Rehderodendron macrocarpum*: a, habit of paniculate inflorescences on a second-year branchlet, $\times \frac{1}{2}$; b, flower (corolla and some stamens removed) showing stamens of two unequal lengths and articulation at base of calyx, $\times 2$; c, woody, ribbed fruit, $\times \frac{1}{2}$; d, cross-section of fruit showing two seeds and fibrous endocarp, $\times \frac{3}{4}$. e, habit of leafy raceme of *Styrax americana*, $\times \frac{1}{2}$. f, g, *S. obassia*: f, flower (note lack of articulation at base of calyx), $\times \frac{3}{4}$; g, longitudinal section of flower showing perigynous insertion of the corolla and epipetalous filaments, $\times 6$. h, i, *S. japonica*: h, habit, showing pendulous fruits, $\times \frac{1}{2}$; i, seed, showing conspicuous basilateral hilum, $\times 2$.

toothed, undulate, or subentire. Corolla usually white, sometimes reddish-brown on the adaxial surface, deeply to shallowly cleft into 5 (rarely 6 or 7) lobes, the corolla tube shorter or rarely longer than the free lobes, insertion hypogynous to perigynous; corolla lobes imbricate or valvate in bud, often stellate-pubescent on the abaxial surfaces, usually spreading or reflexed at anthesis. Stamens 10, the filaments basally connate and adnate to the corolla tube. Gynoecium 3-carpellate; ovary essentially superior to partially inferior, usually adnate to the calyx tube, at least basally, 1–3-locular at base, 1-locular above, with 4–6 ovules per locule; style simple, elongate, terminated by a small, often 3-lobed, capitate stigma. Fruits dry, crustaceous, subtended by the persistent calyx, globose to ovoid-oblong, apically 3-valvate, irregularly dehiscent, or indehiscent. Seeds 1 or rarely 2, subglobose, ovoid, or ellipsoidal, with a conspicuous basilateral hilum, the seed coat hard and smooth, crustaceous, wrinkled, papillate, or stellate-pubescent. TYPE SPECIES: *S. officinale* L. (*Styrax*, the Greek name for the type species and for storax, a resin obtained from that species and used in incense.) — STYRAX, SNOWBELL.

Approximately 120 species of eastern Asia (primarily in tropical and subtropical areas), the West Indies, South and Central America, the Mediterranean region (one species), and North America, where about six species are native. Several species native to the East Indies (not in cultivation in our area) are the sources of the resin benzoin, which is used medicinally as an expectorant, stimulant, and antiseptic, as well as in the manufacture of perfumes and vanilla cream candies. Often termed storax, the resin obtained from species of *Styrax* should not be confused with resins derived from species of *Liquidambar* (Hamamelidaceae), which are known as styrax.

Styrax shirianum Makino of Japan and *S. veitchiorum* Hemsley & Wilson of China were included by Rehder (1940, 1949) but are omitted from the present treatment, since we have found no evidence of their cultivation in our area. Both of these species are grown in England and are attractive ornamentals worthy of cultivation in North America. Moreover, *S. suberifolium* Hooker & Arnott, an evergreen species of China and Taiwan, has been incorrectly recorded as growing at the United States National Arboretum; it is therefore not included here.

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KEY TO THE SPECIES OF STYRAX IN CULTIVATION

1. Inflorescences terminal, few-flowered leafy racemes, the flowers paired (or rarely solitary) terminally, and usually solitary or paired in the axils of subtending leaves. 1. *S. americanum*.
1. Inflorescences few to many-flowered, bracteate, terminal and/or axillary racemes or panicles, often with solitary or fascicled flowers in the axils of subtending leaves. 2.
2. Pedicel and calyx glabrous, 2.5-3.5 cm. long; corolla lobes \pm ovate, 6-8 mm. wide. 2. *S. japonicum*.
2. Pedicel and calyx stellate-pubescent (rarely glabrous), up to 1.8 cm. long; corolla lobes elliptic to ovate, up to, or rarely exceeding, 7 mm. in width. 3.
3. Lower surfaces of the leaf blades densely matted, felted or entirely covered with stellate hairs, the hairs sometimes minute. . . . 4.
4. Lateral and terminal buds concealed by petiole bases; flowers in terminal racemes (7-)12-17 cm. long, often with solitary flowers in the axils of subtending leaves; corolla lobes (1.3-)1.5-2 cm. long. 4. *S. obassia*.
4. Lateral and terminal buds exposed, not concealed by petiole bases; flowers in terminal and/or axillary racemes or panicles less than 10 cm. long, often with solitary or fascicled flowers in the axils of leaves below; corolla lobes less than 1.5 cm. long. 5.
5. Leaf blades (1-)1.5-3(-4) cm. long, (0.5-)1.5-2(-2.5) cm. wide, the majority with irregularly and shallowly lobulate margins above the middle, entire or serrulate below the middle. 8. *S. wilsonii*.
5. Leaf blades (4-)5-11(-16) cm. long, 2-10(-11) cm. wide, the margins entire, serrate, undulate to angulate or occasionally sinuately lobulate. 6.
6. Leaves usually suborbicular to broadly ovate, the margins undulate to angulate and often sinuately lobulate. 7. *S. platanifolium* var. *platanifolium*.
6. Leaves usually elliptic to obovate, the margins entire or serrate. 7.
7. Flowers alternate or paired in inconspicuously bracteate racemes terminating short lateral branchlets, often with smaller axillary racemes or solitary or paired flowers in the axils of leaves below; filaments \pm dense-

- ly stellate-pubescent at base; petioles (3-)5-10 mm. long. 3. *S. grandifolium*.
7. Flowers fascicled as well as occasionally solitary and alternate in bracteate axillary and/or terminal panicles, often with fascicled flowers in the axils of subtending leaves; filaments densely villous at base; petioles 1-3 mm. long. 6. *S. dasyanthum* var. *cinerascens*.
3. Lower surfaces of the leaf blades glabrous or with scattered stellate hairs, primarily along the veins, the surfaces not densely matted, felted or entirely covered by stellate hairs. 8.
8. Flowers in few-flowered axillary racemes (at anthesis the flowers often appearing fasciculate and the racemes terminal); leaves with undulate to angulate and often sinuately lobulate margins. 7. *S. platanifolium* var. *stellatum*.
8. Flowers in several- to many-flowered terminal and/or axillary racemes or panicles, often with solitary or fascicled flowers in the axils of subtending leaves; leaves with subentire, serrate, or denticulate margins. 9.
9. Filaments densely villous at base; petioles 1-3 mm. long; flowers fascicled as well as occasionally solitary and alternate in bracteate axillary and/or terminal panicles, often with fascicled flowers in the axils of subtending leaves. 6. *S. dasyanthum* var. *dasyanthum*.
9. Filaments stellate-pubescent at base; petioles (3-)5-15 mm. long; flowers alternate or paired in inconspicuously bracteate, sometimes basally branched, terminal racemes, often with smaller axillary racemes or solitary or paired flowers in the axils of leaves below. 10.
10. Small trees; calyx densely rusty stellate-pubescent; terminal racemes usually branched basally; raceme rachis subglabrous to finely stellate-pubescent. 5. *S. hemsleyanum*.
10. Shrubs; calyx densely silvery stellate-pubescent; terminal racemes usually simple; raceme rachis densely stellate-pubescent. 3. *S. grandifolium*.

1. *S. americanum* Lamarck, Encycl. Méth. Bot. 1: 82. 1783.

FIGURE 2, e.

Shrubs to 4 m.; young branchlets sparingly stellate-pubescent, becoming glabrous; periderm on older branchlets exfoliating in thin strips, exposing dark, purplish-black or silvery-gray bark. Leaves short-petiolate, the petioles (1-)3-5 mm. long; leaf blades elliptic, oblong, or ovate to obovate, 2-10 cm. long, 1.5-3.5 cm. wide, with acute to short-acuminate apices, obscurely to distinctly serrate margins, and acute bases; upper surfaces of the blades dark green, glabrous to sparingly stellate-pubescent, the lower surfaces pale green, glabrous to densely stellate-pubescent. Flowers in short, few-flowered, leafy racemes, the flowers solitary or usually paired terminally at the ends of short branchlets and solitary or paired in the axils of leaves below; pedicels drooping, slender, the pedicels and

calyces glabrous to densely stellate-pubescent, (7-)9-18 mm. long; corolla lobes oblong-elliptic, 10-12 mm. long, 3-5 mm. wide; stamens included, the styles slightly exserted. Fruits apically 3-valvate, subglobose, 8-10 mm. long, tan; seeds dull reddish-brown, longitudinally grooved, subglobose, 8-10 mm. long, usually 1 per fruit. $2n = 16$. (Including *S. americanum* var. *pulverulentum* (Michx.) Rehder.)

Native to the eastern United States from Pennsylvania southward into Florida and west into Indiana, Illinois, Missouri, Arkansas, and eastern Texas. Both Rehder (1940, 1949) and Gonsoulin (1974) recognized plants with elliptic to ovate or obovate leaves, the petioles and upper surfaces of the blades sparingly stellate-pubescent and the lower surfaces of the blades pulverulent and finely to densely stellate-pubescent, and with densely stellate-pubescent pedicels and calyces as var. *pulverulentum* (Michx.) Rehder in Bailey (Stand. Cyclop. Hort. 6: 3280. 1917) (*S. pulverulentum* Michx., *S. americanum* f. *pulverulentum* (Michx.) Perkins). However, the numerous plants intermediate between var. *americanum* and var. *pulverulentum* attest to Gonsoulin's report (1974) that hybridization and backcrossing occur in localities where the two taxa grow together, and they indicate that recognition of var. *pulverulentum* is not merited.

2. *S. japonicum* Siebold & Zuccarini, Fl. Jap. 1: 53. t. 23. 1835.

FIGURE 2, h, i.

Shrubs or many-branched small trees to 10 m.; young branchlets glabrate, older branchlets with silvery-gray periderm exfoliating in thin strips, exposing reddish- or purplish-brown inner bark. Leaves petiolate, \pm erect or ascending, the blades elliptic-ovate to narrowly oblong, 2.5-8(-12) cm. long, 1.5-3.5(-6.5) cm. wide, with acute, abruptly acuminate, or short-caudate apices (the apex itself often mucronulate), finely serrulate margins (often entire below the middle), and cuneate to attenuate bases, the lamina often decurrent along the sparingly pubescent petiole; upper and lower surfaces of the blades with scattered stellate hairs, principally along the veins. Flowers pendulous, in loose, 3-5-flowered racemes terminating short lateral branchlets, usually with solitary flowers in the axils of subtending leaves; pedicels long and slender, the pedicels and calyces 2.5-3.5 cm. long, glabrous; corolla lobes 9-14 mm. long, 6-8 mm. wide, ovate-elliptic; stamens slightly shorter than the corolla; styles \pm exserted. Fruits subglobose to ellipsoidal, often with a mucronate apex, (9-)10-15 mm. long; seeds 1 or rarely 2 per fruit, ovoidal, reddish-brown, longitudinally 2- or 3-grooved. $2n = 40$. — JAPANESE SNOWBELL.

Native to Japan, China, Korea, Taiwan, and the Philippines. Several varieties and forms, some of questionable validity, have been recognized from over the geographic range of the species, yet none of these variants appear to be in cultivation in our area. This is undoubtedly the most frequently encountered cultivated species of *Styrax*.

3. *S. grandifolium* Aiton, Hort. Kew. 2: 75. 1789.

Shrubs to about 8 m.; young branchlets finely roughened by stellate hairs, the older branchlets with blackish or brownish, finely fissured bark. Leaves petiolate, the petioles (3-)5-11 mm. long; leaf blades elliptic to ovate or typically obovate, 4-10(-20) cm. long, 2.5-7(-12) cm. wide, with short-acuminate or acute apices, subentire or remotely serrulate or denticulate margins, and cuneate to subrounded bases; upper surfaces of the blades pale to dark green, with minute stellate hairs along the veins when young; lower surfaces of the blades glabrous or usually sparsely to densely stellate-pubescent over the entire surface, the pubescence often imparting a silvery- or grayish-green color. Flowers in terminal, bracteate racemes 5-10 cm. long on short lateral branchlets, usually with paired or solitary flowers, or occasionally smaller racemes in the axils of subtending leaves; pedicels and calyces 8-11 mm. long, silvery stellate-pubescent; corolla lobes 10-14 mm. long, 3-4 mm. wide; stamens \pm as long as the corolla, the filaments densely stellate-pubescent at base; styles \pm exserted. Fruits globose, often with an apiculate apex, 7-9 mm. in diameter, apically 3-valvate; seeds 1 or rarely 2 per fruit, subglobose, 7-9 mm. long, dull dark brown. $2n = 32$. — BIG-LEAF SNOWBELL.

Native to the southeastern United States from Virginia and Tennessee southward into Florida, Alabama, Mississippi, Louisiana, and eastern Texas. Plants of *Styrax grandifolium* have been reported to sucker extensively from the roots.

4. *S. obassia* Siebold & Zuccarini, Fl. Jap. 1: 93. *t.* 46. 1835.

FIGURE 2, f, g.

Shrubs or more often small trees to 10 m. with ascending to horizontal branches, usually forming a rounded crown; young branchlets floccose stellate-pubescent, soon glabrous, the periderm on second-year branchlets dark reddish-brown or blackish, exfoliating in thin sheets. Petioles floccose stellate-pubescent, becoming glabrous, the lower portion winged, enclosing the terminal or lateral buds; leaf blades broadly elliptic or more commonly suborbicular or orbicular, 8-16(-20) cm. long, 8-14 cm. wide, with shortly acuminate to rounded apices, subentire to irregularly dentate margins (the teeth apiculate), and rounded to broadly cuneate or truncate bases; upper surfaces of the blades dark green, with stellate hairs along the veins, becoming glabrous; lower surfaces of the blades grayish-green, densely matted with stellate hairs, when young with floccose stellate hairs along the veins. Flowers in drooping terminal racemes (7-)12-17 cm. long on short lateral branchlets, often solitary in the axils of leaves below; pedicels and calyces 1.2-2 cm. long; corolla lobes (1.3-)1.5-2 cm. long, 5-9 mm. wide, elliptic to elliptic-ovate; stamens about as long as the corolla, the styles slightly longer. Fruits (1-)1.5-2 cm. long, subvoid to conical, often with a short, rostrate apex, the surface

longitudinally wrinkled, grayish- or greenish-white; seeds 1 per fruit, \pm ovoid, ca. 1.5 cm. long, dull reddish-brown. $2n = 16$.

Native to Japan, China, Korea, and Manchuria. The beautiful large racemes, often partially hidden by the large leaves, and the handsome habit of the plants make this species deserving of wider use as an ornamental.

5. *S. hemsleyanum* Diels, Bot. Jahrb. 29: 530. 1901.

Trees (or shrubs?) to ca. 10 m., young branchlets sparingly stellate-pubescent, soon glabrous, the periderm on older branchlets exfoliating in thin, longitudinal strips, exposing grayish- or reddish-brown inner bark. Leaves petiolate, the blades ovate, obovate, broadly elliptical, or lanceolate, 6–10.5(–13) cm. long, 2.5–6.5(–9) cm. wide, with remotely serrulate to finely serrate or denticulate margins, abruptly acuminate (or rarely rounded) apices, and broadly cuneate to rounded bases; lower surfaces of the blades reticulate, glabrate, or with scattered stellate hairs along the veins. Flowers in remotely bracteate terminal racemes on short lateral branchlets, the racemes (4–)6–13.5 cm. long, often branched below and often with smaller racemes in the axils of subtending leaves; pedicels and calyces 0.8–1.2 cm. long, the calyx tubes densely stellate-pubescent and with large, darker stellate hairs scattered over the surface; corolla lobes elliptic, 0.9–1.5 cm. long, 4–5 mm. wide; stamens included, the styles \pm equalling the corolla. Fruits oblong-ovoid, 1–1.3 cm. long, dehiscent into 3 valves from the apiculate apex; seeds 1 per fruit, ovoid-acute, reddish-brown, ca. 1–1.2 cm. long, the seed coat often with 1 or 2 shallow longitudinal grooves.

Native to Honan, Hupeh, and Szechwan provinces in central China.

6. *S. dasyanthum* Perkins, Bot. Jahrb. 31: 485. 1902.

Shrubs or small trees to 8 m.; young branchlets finely stellate-pubescent, becoming glabrous, the periderm on older branchlets exfoliating in thin strips, exposing dark reddish- or purplish-brown bark. Leaves sessile to short-petiolate, the petioles 1–3 mm. long; leaf blades elliptic, broadly elliptic, or obovate, (2–)4–13.5 cm. long, (1.5–)2–6(–7) cm. wide, with finely serrate margins, cuneate to rounded bases, and acute, acuminate, or abruptly acuminate apices; upper surfaces of the leaf blades glabrous or with scattered stellate hairs primarily along the midvein; lower surfaces of the blades with scattered stellate hairs primarily along the veins and in the axils of the midvein and lateral veins. Flowers solitary and fascicled in bracteate panicles 6–8 cm. long terminating short lateral branchlets, with solitary, paired, or fascicled flowers in the axils of subtending leaves; pedicels and calyces 8–12(–14) mm. long; corolla lobes lanceolate, (7–)9–11 mm. long, ca. 2 mm. wide; stamens \pm as long as the corolla, the filaments densely villous at base; styles slightly

exserted. Fruits ovoid, 8–11(–15) mm. long, often with a rostrate apex; seeds 1 per fruit, reddish-brown, the seed coat finely wrinkled.

Native to central China. The majority of herbarium specimens of this species from cultivation in North America are referable to var. *cinerascens* Rehder (Pl. Wilsonianae 1: 289. 1912), which was based on a plant from Hupeh Province. Plants of var. *cinerascens* differ from plants of var. *dasyanthum*, described above, in the dense stellate pubescence of the young branchlets and in the matted stellate pubescence of the lower surfaces of the leaf blades.

7. *S. platanifolium* Engelman ex Torrey, Smithsonian Contr. Knowl. 6: 4, *in nota*. 1853.

Many-branched small trees or shrubs to 4 m.; young branchlets finely or remotely stellate-pubescent, the periderm on older branchlets exfoliating in thin, longitudinal strips. Leaves petiolate, the petioles 5–10 (–13) mm. long; leaf blades suborbicular to broadly ovate, (1.5–)2.5–8 cm. long, (1.5–)2–9 cm. wide, with subcordate, rounded, truncate, or obtuse bases and undulate to angulate, often sinuately lobulate margins; upper surfaces of the leaf blades dull green, glabrous, the lower surfaces glabrous or with scattered hairs along the conspicuously reticulated veins. Flowers in short, 3–5-flowered, \pm drooping, axillary racemes, the racemes often appearing terminal and the flowers often appearing fasciculate at anthesis; pedicels and calyces 8–12(–18) mm. long, glabrous or finely puberulent; corolla lobes 12–14(–15) mm. long, 4–6 mm. wide; stamens included, the style slightly exserted. Fruits globose or subglobose, 7–8 mm. in diameter, apically 3-valvate, the slender style often persistent; seeds 1 per fruit, globose, ca. 7 mm. in diameter, orangish-brown.

Endemic to limestone canyons of the Edwards Plateau of Texas. Plants with the lower surfaces of the leaf blades and the pedicels and calyces thinly to densely stellate-pubescent have been recognized as var. *stellatum* Cory (Madroño 7: 111. 1943). Although *Styrax platanifolium* is reported as cultivated at the Henry Foundation for Botanical Research, Gladwyne, Pennsylvania, it is not known whether var. *platanifolium*, var. *stellatum*, or both are represented in the collections there.

8. *S. wilsonii* Rehder, Pl. Wilsonianae 1: 293. 1912.

Small, many-branched shrubs to ca. 2 m.; young branchlets densely stellate-pubescent, older branchlets with finely fissured, purplish-black bark. Leaves sessile to short-petiolate, the petioles 1–3 mm. long; leaf blades broadly elliptic to rhomboid, (1–)1.5–4 cm. long, (0.5–)1.5–2.5 cm. wide, with acute to acuminate apices, irregularly and shallowly lobulate margins (often subentire below the middle), and cuneate bases; upper surfaces of the blades green, with stellate hairs along the veins, the lower surfaces grayish, densely matted with stellate hairs, often with

additional rusty stellate hairs along the veins. Flowers on very short lateral branchlets, in 3–5-flowered, bracteate, terminal racemes and occasionally in the axils of the few leaves below; pedicels and calyces 6–8 mm. long, the calyx densely stellate-pubescent, with larger rusty stellate hairs superimposed and scattered over the surface; corolla lobes 7–8 mm. long, 2–3 mm. wide, elliptic; stamens \pm as long as the corolla; styles slightly exserted. Fruits subglobose, ca. 5 or 6 mm. in diameter, the subtending calyx persistently stellate-pubescent; seeds ovoid-subglobose, 5–6 mm. long, reddish-brown. (*S. wilsonii* Rolfe.)

Apparently endemic to western Szechwan Province, China.

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